

# CLASSIFICATION OF THE ECHINODERMATA

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**ABSTRACT.** A critical review of past attempts to classify echinoderms is presented and it is shown that, in retrospect, fossil groups have been incorporated into classifications in an arbitrary manner that has confused rather than clarified. The search for relationship through the recognition of pattern in character distribution has become progressively divorced from the production of classification schemes, and the most recent classifications are the most ambiguous about relationships. Furthermore, the increased knowledge we have gained about fossil echinoderms has added very little to our understanding of how extant groups are interrelated and, indeed, has sometimes been interpreted misleadingly. It is argued that fossils cannot generally provide insight into the relationships of living groups except where characters have been lost through developmental foreshortening. The most important taxonomic information that palaeontology can provide concerns the pattern of character acquisition within the stem group, although it can also be useful in providing the latest date by which a split occurred, and in checking statements of homology and identifying synapomorphic characters that have been lost in one or other sister group. It is concluded that the higher classification of the Echinodermata should be based first and foremost on the distribution of characters gleaned from the study of embryology and comparative anatomy in living echinoderms. Fossil groups can then be added to this classification in their appropriate place.

An analysis of character distribution amongst the five extant classes of echinoderm shows that the Eleutherozoa form a monophyletic group whose primitive sister group is the Pelmatozoa. Within the Eleutherozoa, asteroids are the primitive sister group to the group (ophiuroids + echinoids + holothuroids) for which the name *Cryptosyringida* is proposed. The relationship of holothuroids within the cryptosyringids is more ambiguous but it is concluded that echinoids and holothuroids are sister groups and more closely related to one another than either is to the ophiuroids. A phylogenetic classification is proposed and this provides the primary framework into which fossil groups can be incorporated by using the concept of stem and crown groups. The position of principal fossil groups within this classification is briefly outlined and outstanding problems for future research are identified.

WITHIN the last few years, systematics, the study of biological classification in accordance with natural relationships, has undergone a rigorous scrutiny of its methodological basis. This debate has been fought largely, though not entirely, amongst zoologists and vertebrate palaeontologists and a vast literature now exists discussing the virtues and vices of phyletic, phenetic, and gradistic methods of classification. This debate has done nothing but good for the science of systematics and I feel that cladistic methodology has proved itself the most internally consistent and the most informative method of organizing data on character distribution. My interests lie in unravelling the phylogeny of echinoderms and producing a classification that reflects this. The phylogeny can be inferred from analysis of character distribution which can be presented in the form of a branching diagram (cladogram) and the most informative classification is one that follows the hierarchical pattern revealed by the cladogram. However, I shall not discuss the merits of cladistics over other methods of classification since there is more than enough written on this subject already. Those unfamiliar with the ideas of cladistics and how they compare with more traditional methods may read one of the many books that have recently appeared on the subject (e.g. Eldridge and Cracraft 1980; Nelson and Platnick 1981; Wiley 1982).

While arguments have raged in systematic zoology, the systematics of fossil invertebrates, as reflected in the pages of this journal, has continued much as before. Of course, some articles using cladistic methodology have appeared but there is still the prevailing feeling that the fossil record holds the key to understanding relationships. But this belief has been challenged. Fossils, it is said, are irrelevant in determining biological relationships (Kitt 1974; Løvtrup 1977) or play only a minor role

(Patterson 1982). If these challenges are correct then systematic palaeontologists must not only reassess their methodology but also their aims.

This paper takes a critical look at the way in which echinoderms (particularly fossil echinoderms) have been classified, outlines what their fossil record can and cannot tell us, and suggests how they might be classified more informatively. Few, if any, of the ideas are new (although they have not been applied to fossil echinoderms before) but I feel it is important to make a clear statement of the methodology employed when recommending a fairly drastic change to the classification of echinoderms.

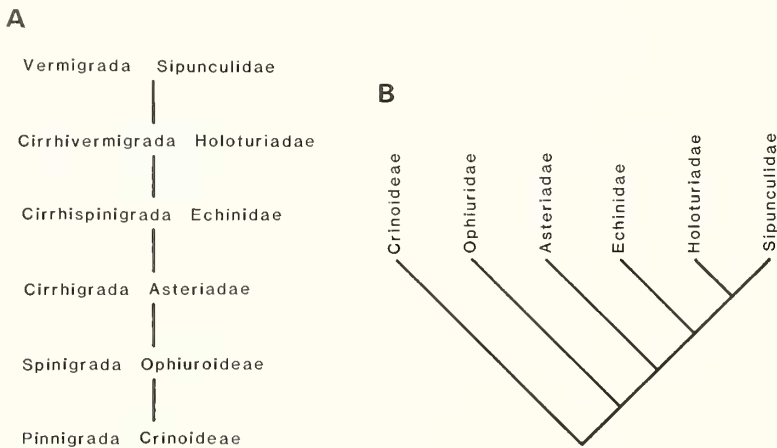
THE EVOLUTION OF ECHINODERM CLASSIFICATION

It is most instructive to follow the way in which the classification of echinoderms has altered as our knowledge of fossil echinoderms has improved. Echinoderms were not recognized as a natural group until 1791 when Bruguière subdivided Linnaeus's class Vermes in which they had previously been put. Bruguière included asteroids, ophiuroids, and echinoids in his order Echinodermata but failed to recognize holothuroids as echinoderms. In 1801 Lamarck added holothuroids to the Echinodermata but grouped them with medusoid coelenterates in the class Radiata. Twenty years later Miller (1821) formally separated a group Crinoidea for stalked echinoderms that had previously been placed with the starfish in the group Stellerides. Thus by 1821 the five classes of living echinoderm had all been recognized.

As an example of an early attempt to classify echinoderms I shall use the scheme proposed by Forbes (1841). He did not consider fossil forms and on the basis of comparative anatomy proposed the following grade classification:

- (i) Pinnigrada—Crinoideae
- (ii) Spinigrada—Ophiuroideae
- (iii) Cirrhigrada—Asteroideae
- (iv) Cirrhispinigrada—Echinidae
- (v) Cirrhivermigrada—Holoturiidae
- (vi) Vermigrada—Sipunculidae

Forbes based his classification on what he identified as a 'progression of organization' from polyps to vermes starting with crinoids and ending with sipunculids and he referred to it as a procession through 'forms gradually changing character'. This pre-Darwinian view of echinoderm relationships can be summarized as a gradistic tree (text-fig. 1A) and translated into a fully resolved cladogram (text-fig. 1B). Forbes then was very specific about how he thought echinoderm groups were related (though, of course, not necessarily correct) and used a classification scheme which reflected this.

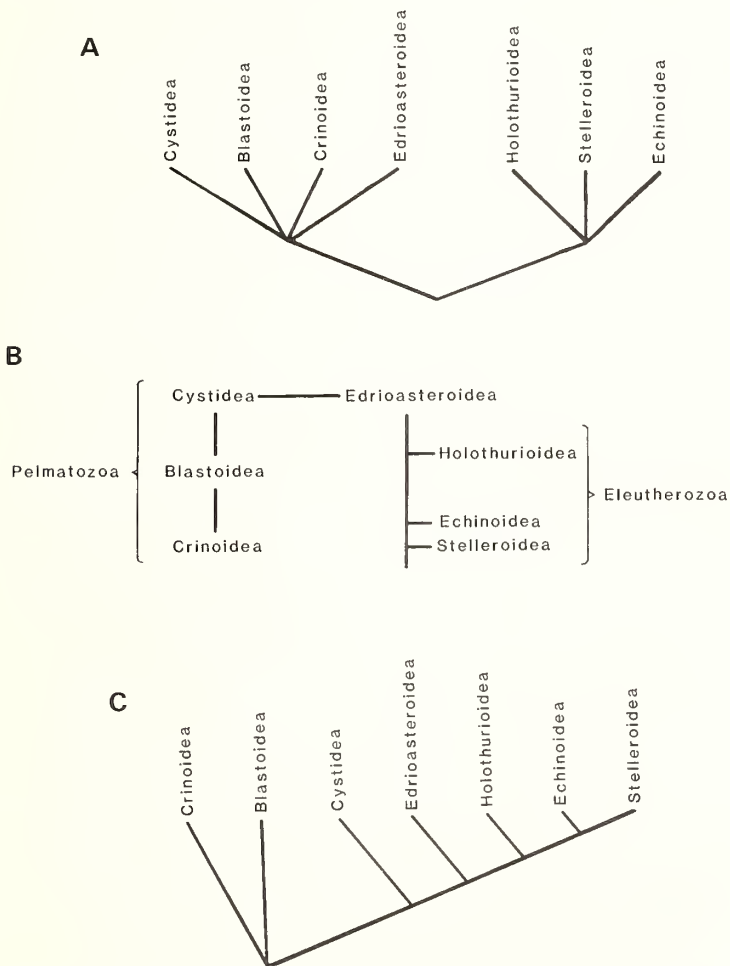


TEXT-FIG. 1. Interrelationships of echinoderm groups according to Forbes (1841). A, Forbes's gradistic classification scheme. B, the cladogram derived from the classification.

In the second half of the nineteenth century great strides were being made in both embryology and palaeontology and in 1900 Bather published a major account of Recent and fossil echinoderms in which he proposed the following classification:

- |  |  |
|--|--|
| Grade A Pelmatozoa<br>Class I Cystidea<br>Class II Blastoidea<br>Class III Crinoidea<br>Class IV Edrioasteroidea | Grade B Eleutherozoa<br>Class I Holothurioidea<br>Class II Stelleroidea<br>Subclass Asteroidea<br>Subclass Ophiuroidea<br>Class III Echinoidea |
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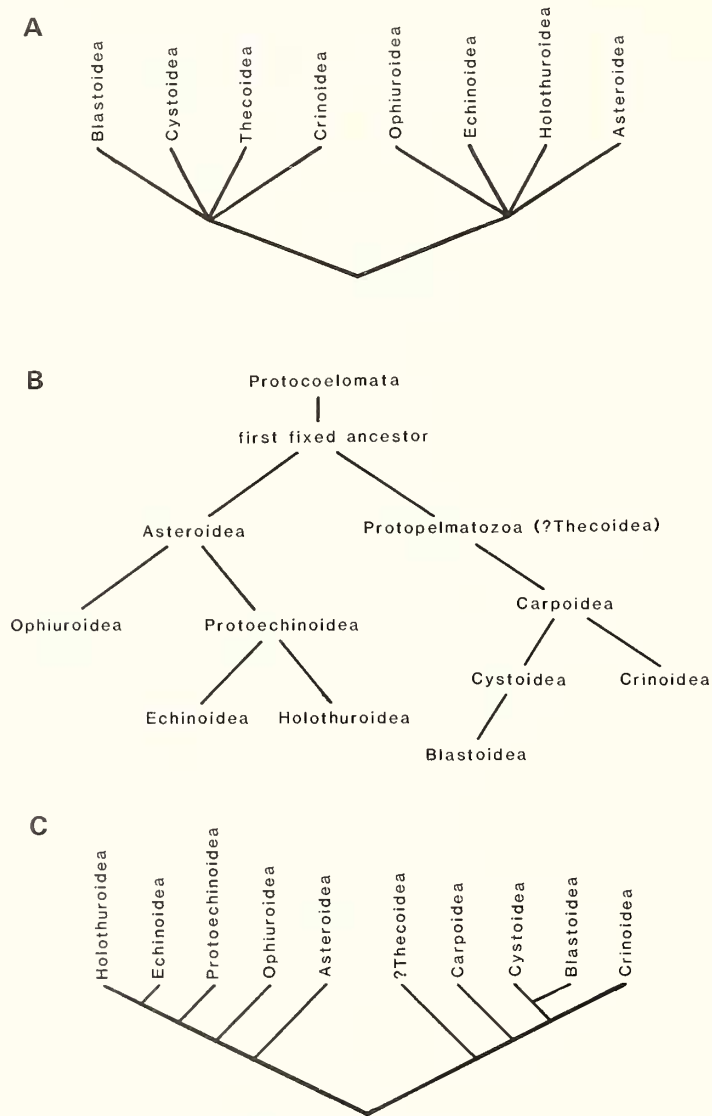
Bather's classification identifies three components within the Echinodermata (text-fig. 2A): a group Pelmatozoa, a group Eleutherozoa, and a group Stelleroidea. This is compatible with any of forty-five fully resolved statements of relationship. In addition, he presented a diagram which summarized his views on how these groups were related phylogenetically (text-fig. 2B) which can be transformed



TEXT-FIG. 2. Interrelationships of echinoderm groups according to Bather (1900). A, the information concerning relationship that is conveyed in Bather's classification. B, his diagram showing how he thought the various groups were related to one another. C, a phylogram derived from B.

into a phylogram (text-fig. 2C). Comparing the classification and phylogeny shows that Bather used a classification that conveyed some but not all of the phylogenetic information.

Bather's scheme made three changes to the previous scheme of Forbes, two of which stem from the growth in knowledge about fossil echinoderms. Palaeontology showed that living crinoids were only a small remnant of a once much larger and more diverse group of stemmed echinoderms. Bather recognized three fossil groups in addition to crinoids, placing the whole lot in the subphylum Pelmatozoa. He also realized that the other living groups were more advanced in being unattached



TEXT-FIG. 3. Interrelationships of echinoderm groups according to MacBride (1906). A, the information concerning relationship that is conveyed in MacBride's classification. B, his diagram of echinoderm phylogeny. C, a phylogram derived from B.

and grouped them together in the subphylum Eleutherozoa. Secondly, Bather chose to group asteroids and ophiuroids together because fossils existed that were intermediate in form making any distinction based on character distribution in living groups unworkable. The illogicality of this view is discussed later. Finally, he reinterpreted holothuroids as the most primitive living eleutherozoans, not the most advanced, on the basis of embryological data. Bather recognized holothuroids to be 'primitive with respect to Pelmatozoic structures, specialised as regards eleutherozoic' but chose to emphasize the symplesiomorphic aspects of holothuroid development which, in retrospect, was a misjudgement.

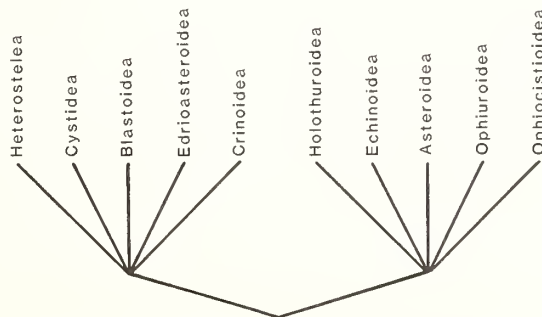
We can contrast the approach taken by Bather, who was a palaeontologist, with that of MacBride, an embryologist. MacBride (1906, 1914) considered the phylogenetic significance of echinoderm development without reference to the fossil record. He used a classification scheme that was identical to Bather's except that asteroids and ophiuroids were separated at class level. His classification then identifies just two components (text-fig. 3A). MacBride (1906) illustrated how he believed the various echinoderm groups were related in a diagram (text-fig. 3B) which can be translated into a fully resolved phylogram (text-fig. 3C). Although MacBride chose a classification whose structure contained little of the information he had gleaned from embryology, he was able to make a positive contribution by reversing the position of asteroids and ophiuroids as set out by Forbes. He did this by recognizing that embryologically ophiuroids were more advanced than asteroids.

Throughout this century palaeontologists have continued to discover and describe new fossil groups and in 1955 Hyman published her excellent review of echinoderms with the following classification:

Subphylum Pelmatozoa	Subphylum Eleutherozoa
Class Heterostealea	Class Holothuroidea
Class Cystidea	Class Echinoidea
Class Blastoidea	Class Asteroidea
Class Edrioasteroidea	Class Ophiuroidea
Class Crinoidea	Class Ophiocystioidea

Two previously known fossil groups have been elevated to class level, the carpoids (Heterostealea) and the ophiocystioids making ten classes in all. In the text Hyman seems to accept MacBride's views on echinoderm relationships yet the classification identifies just two categories higher than class level (text-fig. 4) and is consistent with over 11,000 possible fully resolved phylogenetic schemes. Thus it is relatively uninformative.

Recently, there has been a dramatic increase in the number of minor fossil groups each containing a small number of distinctive species that have been elevated to high categorial rank. In the *Treatise on*



TEXT-FIG. 4. The information concerning relationship that is conveyed in the classification of Hyman (1955).

*Invertebrate Paleontology* (Moore and Teichert 1978) a total of twenty-one classes, sixteen of which are extinct, are arranged into four subphyla as follows:

Subphylum Homalozoa	Subphylum Asterozoa
Class Ctenocystoidea	Class Stelleroidea
Class Stylophora	Subclass Somasteroidea
Class Homostealea	Subclass Asteroidea
Class Homoiostealea	Subclass Ophiuroidea
Subphylum Crinozoa	Subphylum Echinozoa
Class Eocrinoidea	Class Helicoplacoidea
Class Rhombifera	Class Camptostromatoidea
Class Diploporita	Class Edrioasteroidea
Class Blastoidea	Class Edrioblastoidea
Class Parablastoidea	Class Cyclocystoidea
Class Paracrinoidea	Class Ophiocystoidea
Class Crinoidea	Class Echinoidea
	Class Holothuroidea

This classification relies heavily on the work of Fell (1945, 1962, 1963, 1965, 1967) who rejected embryology as a guide to relationships and in its place attempted to use fossils as the guiding criterion. The results of this departure can be seen in the marked increase in uncertainty about relationships. The information content contained in the classification has also decreased significantly (text-fig. 5). Just four components are recognized leaving five polychotomies and this scheme is consistent with over  $2 \times 10^{11}$  possible statements of relationship!

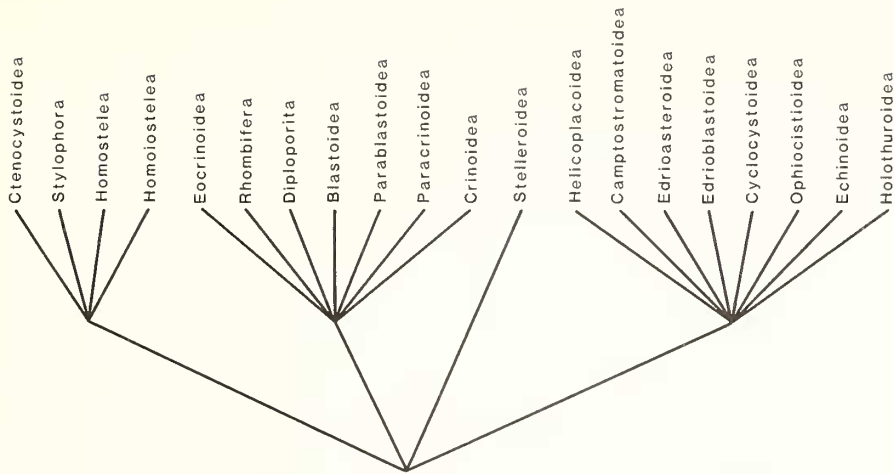
An alternative classification has been proposed by Sprinkle (1980) who recognized a fifth subphylum, as follows:

Subphylum Crinozoa	Subphylum Echinozoa
Class Crinoidea	Class Edrioasteroidea
Class Paracrinoidea	Class Edrioblastoidea
Subphylum Blastozoa	Class Cyclocystoidea
Class Eocrinoidea	Class Helicoplacoidea
Class Rhombifera	Class Ophiocystoidea
Class Diploporita	Class Echinoidea
Class Parablastoidea	Class Holothuroidea
Class Blastoidea	Subphylum Homalozoa
Subphylum Asterozoa	Class Stylopora
Class Asteroidea	Class Homoiostealea
Class Ophiuroidea	Class Homostealea
	Class Ctenocystoidea

The information content of this classification is better, but only marginally so (text-fig. 6). Five components are identified leaving four unresolved polychotomies and the classification is consistent with over  $1.7 \times 10^9$  different statements of relationship.

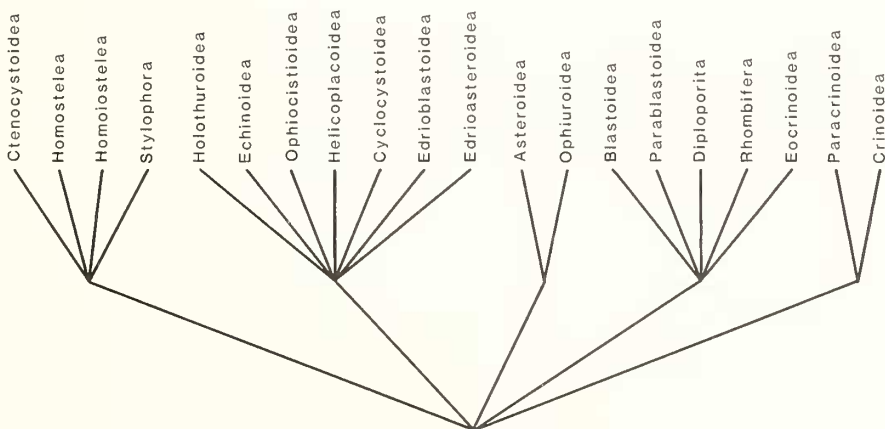
So what conclusions are to be drawn from the way in which echinoderms have been classified in the past? Forbes provided a classification in which his ideas of relationship, as revealed by morphological organization, were clearly specified. Since then there has been a progressive decrease in the information about relationships that is incorporated into classification schemes, despite an increasing understanding of embryology and palaeontology. The growth of knowledge concerning embryology led to the construction of clearly defined phylogenetic hypotheses and corroborated all but one of Forbes's findings. By showing that of the four extant classes of eleutherozoans, asteroids have the most generalized development and are therefore more primitive than ophiuroids, embryology made a positive contribution to our knowledge of relationships.

The increased knowledge of the fossil record seems to have had no such beneficial effect. The result



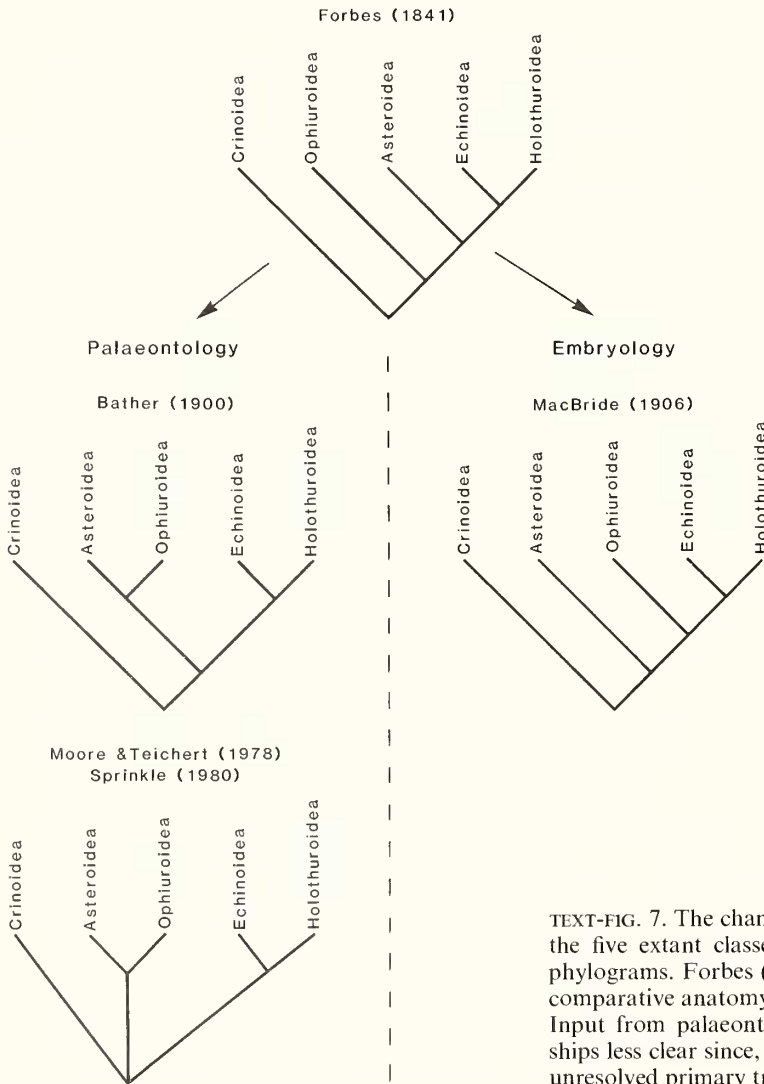
TEXT-FIG. 5. The information concerning relationship that is conveyed in the *Treatise* classification (Moore and Teichert 1978).

of discovering more and more fossil groups that have some characteristics that set them apart from living groups has been to add to the general confusion. By elevating these fossil groups to high taxonomic rank, the hierarchical arrangement of Linnaean classification has been largely destroyed and its most important attribute, its information content, greatly reduced. The most recent classifications are also the least specific about character distribution amongst the groups they recognize. The obvious question then arises—is our increasing uncertainty about relationships in echinoderms real or is it an artefact of the way in which data, particularly palaeontological data, have been handled? If the former is correct and the more fossils we continue to find the more confused our ideas of relationship become, then palaeontology can have nothing to contribute to this subject. However, the confusion that has arisen is attributable to two causes, misinterpretation of what the fossil record tells us and an inappropriate taxonomic methodology. The following two examples are given in illustration.



TEXT-FIG. 6. The information concerning relationship that is conveyed in the classification of Sprinkle (1980).

1. *The position of ophiuroids in relation to other echinoderms.* The clearest example of how the fossil record has been misinterpreted comes from the way in which ophiuroids have been linked with asteroids. Most zoologists who have considered the relationship of ophiuroids to other echinoderms have been so struck by the fact that ophiuroids and echinoids pass through very similar developmental stages that are advanced compared to those in asteroids, that they believe ophiuroids and echinoids to be more closely related (e.g. Hyman 1955). Yet amongst many palaeontologists from Bather onwards there has been a clear belief that the fossil record shows asteroids and ophiuroids to be more closely related and distinct from echinoids (text-fig. 7). This has led some palaeontologists to claim that embryology is misleading and best ignored (e.g. Fell 1967) whilst some zoologists flatly refuse to believe that the fossil record can be correct (e.g. Hyman 1955). What then does the fossil record show? Excellent work by Schondorf, Schuchert, and Spencer has shown that, in the lower Palaeozoic, asteroids and ophiuroids are much less distinct from one another (i.e. they have fewer autapomorphies) and that indeed there are some forms so generalized (primitive) in form that



TEXT-FIG. 7. The changing ideas of relationship amongst the five extant classes of echinoderm, in the form of phylograms. Forbes (1841) based his ideas primarily on comparative anatomy, MacBride (1906) on embryology. Input from palaeontology has actually made relationships less clear since, in recent classifications, there is an unresolved primary trichotomy.



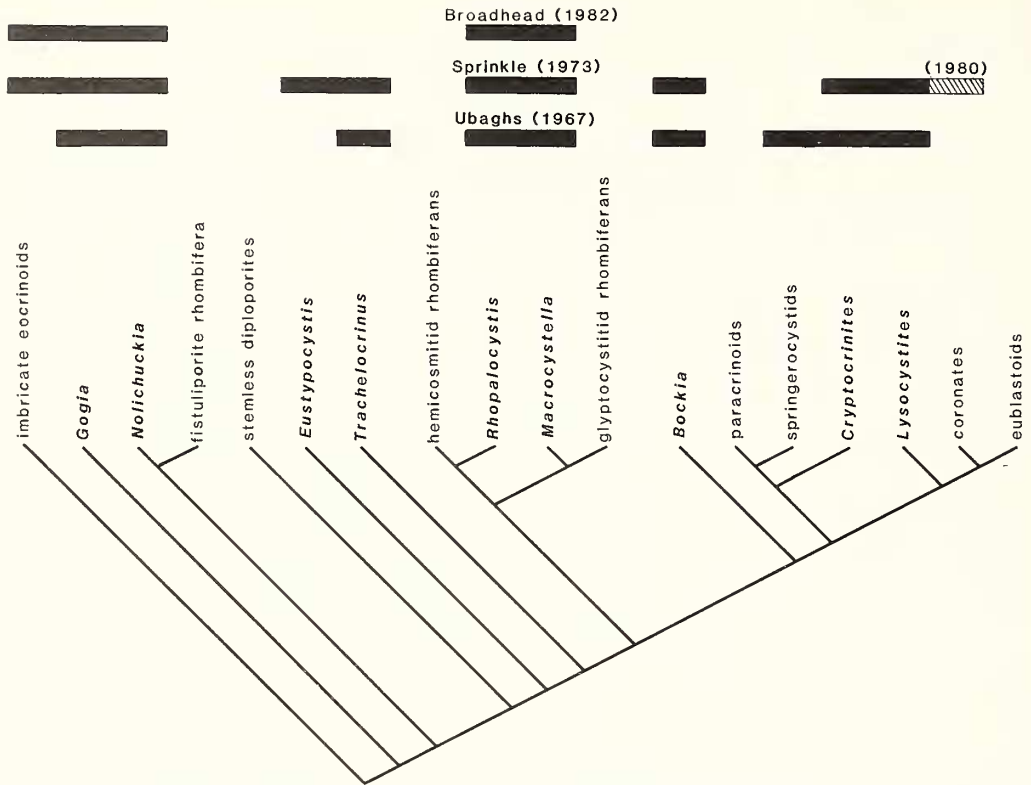
they can be interpreted as ancestors to both asteroids and ophiuroids. This led to the claim that because the fossil record proves that asteroids and ophiuroids stemmed from a common ancestor they must be more closely related compared to echinoids, whose origins are still largely unknown palaeontologically (e.g. Nichols 1968).

It may come as some surprise then to realize that the two views are not contradictory but complementary. Both embryological and palaeontological observations are in complete agreement; it is only the interpretation placed on the palaeontological data that is at fault. The fossil record shows that asteroids and ophiuroids share a common ancestry—but this is also predicted from embryological evidence (see text-fig. 7). Embryological data make a further prediction: that echinoids and ophiuroids shared a common ancestor that was not also shared with asteroids, i.e. that some of the so-called primitive ophiuroids will turn out to be generalized enough to have been ancestral to both living ophiuroids and living echinoids. Surprisingly, the implications of the embryological data have not been realized before now and the absence of obvious fossil evidence has been taken as sufficient proof for rejecting the wealth of zoological data. The question which has never before been addressed and which is only now beginning to be investigated concerns which of the 'primitive ophiuroids' are true ophiuroids and which are so generalized in morphology that they are best considered as ancestors to both living ophiuroids and living echinoids.

2. *The classification of eocrinoids.* As an example of what could be considered to be misdirected taxonomic endeavour I shall discuss the way in which eocrinoids, a primitive group of cystoids, have been classified. Eocrinoids were first recognized as a distinct group by Jaekel (1918), who believed them to be primitive crinoids. More recent work has clearly identified them as cystoids *sensu lato* (= Blastozoans), and there seems to be complete agreement amongst all workers that eocrinoids are the most primitive group of cystoids from which all the other cystoid groups evolved: the 'root stock' of other cystoid groups to use gradistic terminology. More than any other pelmatozoan group, eocrinoids have been difficult to diagnose satisfactorily. For example, one of the most thorough and detailed reviews of the eocrinoids was carried out by Sprinkle (1973), yet his diagnosis for the Class Eocrinoidea is as follows: 'Early blastozoan echinoderms having an irregularly adjacent or imbricately plated globular or flattened calyx, with or without epispines, an irregularly multiplied holdfast or a true stem as an attachment appendage [except for Lichenoididae], a primitive ambulacral system bearing normal or modified brachioles and usually little pentameral symmetry' (Sprinkle 1973, p. 58).

The only unifying characteristic of this group of pelmatozoans seems to be 'primitiveness'. Indeed, the Eocrinoidea includes a heterogeneous assemblage of species whose only similarity is that they lack the autapomorphic characteristics of the other, less ambiguously defined, cystoid groups. As such, they are simply what remains of the Cystoidea once species with diplopores (Diploporita), rhombs (Rhombifera), hydrospires (Blastoidea), and asymmetrical thecas with uniserial ambulacra and brachioles (Paracrinoidea) have been removed, and cannot possibly represent a natural (i.e. monophyletic) grouping.

Largely because it is difficult to give any satisfactory diagnosis for the Eocrinoidea (because they are not a natural group) there has been a great deal of futile argument about precisely which species should be included in, and which rejected from, the 'Class' Eocrinoidea. Simply taking some of the changes that have been proposed since the *Treatise* (Ubaghs 1967) will show how much disagreement exists. Paul (1968), for example, removed *Macrocystella* from the eocrinoids and grouped it with glyptocystitid rhombifera, but Sprinkle (1973) rejected it as a rhombiferan and returned it to the eocrinoids; arguments about this still continue. *Springerocystis*, *Columbocystis*, and *Foerstecystis* were removed from the eocrinoids by Sprinkle (1973) who placed them with paracrinooids. Parsley and Mintz (1975), however, objected to them being paracrinooids and returned them to the eocrinoids. Recently the coronates, which were originally grouped together with blastoids (Regnéll 1945) and which were later transferred to inadunate crinoids by Fay (1978), have been added to the eocrinoids by Sprinkle (1979, 1980). Broadhead (1982) has added to the general confusion still further by rejecting all those species without epispines from the eocrinoids without making any positive contribution as to how the rejected taxa ought to be classified.



TEXT-FIG. 8. A phylogram showing the relationships of a number of cystoid groups taken from the phylogenetic tree given by Paul in Paul and Smith (1984). Three alternative views of what constitutes the 'Class Eocrinoidea' are shown. As eocrinoids are a paraphyletic grouping of primitive cystoids their boundaries are inevitably arbitrary.

The arbitrary way in which eocrinoids have been grouped becomes obvious when the various alternative schemes are plotted on a phylogram of cystoid groups (text-fig. 8). Clearly there will always be arguments as to where boundaries are to be drawn for such a subjective and paraphyletic group as the 'Eocrinoidea'. Such arguments about what constitutes a paraphyletic group are not only futile (since unnatural groups will always be arbitrary) but are a positive hindrance to discovering relationship amongst cystoids.

An understanding of how the various cystoid groups are related will become much easier if the 'Class' Eocrinoidea is abandoned and its members allocated to appropriate monophyletic groups. Although this will necessitate the creation of new taxa or the redefinition of old taxa, it will lead to a much clearer and very much more precise view of cystoid evolution. Here, then, is an example where misdirected taxonomic endeavour has actually hindered growth of knowledge concerning the relationships of cystoid groups.

#### CHARACTER DISTRIBUTION AND THE INFORMATION CONTENT OF CLASSIFICATIONS

Before discussing the positive contribution that the fossil record can make to phylogenetic analysis, it is worth while outlining the concept of stem and crown groups which was first developed by Hennig (1966, 1981). Identifying pattern in the distribution of morphological characters is the

essence of recognizing relationship. Derived characters shared amongst two or more species are synapomorphies that indicate phylogenetic kinship, those unique to one species or one group of species are referred to as autapomorphies. Obviously a character that is a synapomorphy uniting a group of species can also be thought of as an autapomorphy of that group as a unit.

The presence of derived characters shared amongst two or more species is usually taken as an indication of phylogenetic kinship. This is not to say that convergence does not occur. Convergence can only be recognized on the pattern of character distribution, since to suggest that a derived character found in two species is a convergent feature requires that at least two further derived characters are known that link one of those species to a group that does not include the other species. Evolutionary convergence is invoked where there is incongruence in character distribution and parsimony is used to determine which characters are true synapomorphs and which due to convergence.

Any monophyletic group with both living and fossil species can be divided into two parts—a crown group and a stem group. The crown group contains the latest ancestor common to all living members of that group together with all of its descendants. They are recognizable as crown group members because they possess all of the synapomorphies that unite the living members and form a monophyletic group. The stem group contains only fossil species and is a paraphyletic assemblage. They are identified as stem group members since they will have at least one, but not all, of the autapomorphies of the crown group. In phylogenetic terms, the stem group consists of all those species to evolve after the group had separated from its living sister group but prior to the evolution of the latest common ancestor of the crown group. The importance of differentiating between crown and stem groups will become apparent later.

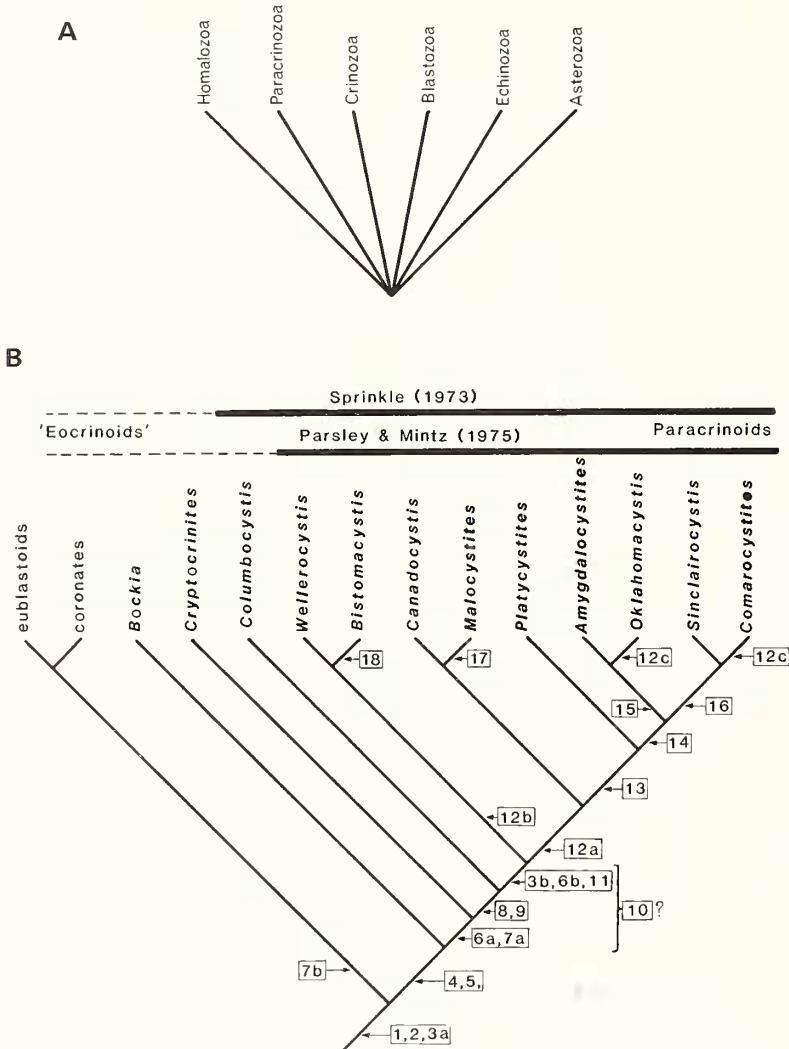
A 'natural' classification scheme is best considered as a method of conveying information about character distribution. Both character distribution and the Linnaean system of classification have the form of a nested hierarchy. Maximum information about character distribution is conveyed when the hierarchical pattern of the classification exactly matches the pattern of character distribution. Unfortunately, past classification schemes have not been as informative as they might be and the recent predilection for erecting notional class status for small problematic groups of fossil echinoderms has had a most detrimental effect on the information content of classifications by destroying the hierarchical arrangement.

In support of small fossil groups of high categorial rank Sprinkle (1975, 1980) and Paul (1979) have argued that it is a true reflection of an early diversity of form in echinoderm evolution. Even if this is so, it is no reason for elevating a large number of groups within one taxon to the same categorial rank since this is uninformative about character distribution within the higher taxon. Their preferred classifications are based not on the distribution of shared characteristics, but on the development of prominent autapomorphies (hence the necessity for a 'class' Eocrinoidea for all those cystoids left once other groups have been distinguished on autapomorphies). The presence of autapomorphies provides no information about the relationships with other groups. Unlike Breimer and Ubaghs (1974), it is not the taxonomic rank that I primarily object to but the purely subjective way in which a large number of groups are given the same rank within a large taxon. This procedure is not only arbitrary but makes no contribution to the search for pattern in character distribution and hence relationship.

The illogicality of this approach can be illustrated by the recent creation of a sixth subphylum of echinoderms, Paracrinozoa, by Parsley and Mintz (1975). There are just eight genera of paracrinozoa (seven when Parsley and Mintz erected the subphylum), all of which have a distinctively asymmetrical theca and uniserial free appendages. Prior to this paracrinozoa had always been considered cystoids, but Parsley and Mintz thought that the group had characteristics which were in part cystoid (stem and theca) and in part crinoid (subvective system). Given that they are correct in their interpretation, then paracrinozoa, crinozoa, and cystoids must form a phylogenetically closely related group within the Echinodermata, a fact which Parsley and Mintz acknowledged. Yet by elevating the paracrinozoa to subphylum rank they are in effect stating that it is as closely related morphologically to carpozoa

(Homalozoa), sea stars (Asterozoa), and Echinozoa as it is to either cystoids (Blastozoa) or crinoids (text-fig. 9A).

In my opinion Parsley and Mintz were mistaken in their identification of the free appendages as crinoid arms and pinnules. There is a great deal of confusion about the homology of pelmatozoan appendages which Paul and Smith (1984) have tried to clear up. In crinoids the entire subvective system is derived from ambulacra as a whole, whereas in cystoids many of the free appendages are brachioles derived from just cover-plate series. Paracrinozoa have free or recumbent uniserial ambulacra ('arms') which give rise to free uniserial brachioles. Similar structures are known in other



TEXT-FIG. 9. The status of paracrinozoa. A, the implied relationship of paracrinozoa to other echinoderm groups in the classification proposed by Parsley and Mintz (1975). B, a cladogram for the better-known paracrinozoa and some related 'eocrinoids' to show how analysis of character distribution leads to a clear statement about the status of paracrinozoa within the cystoids. Characters 1-18 are stated in Table 1.

cystoids: uniserial appendages are found in diploporite cystoids while free or recumbent ambulacra with brachioles are found in many cystoids such as the eocrinoid *Bockia*, glyptocystitid rhombiferans, coronates, and blastoids. Sprinkle (1973) quite correctly pointed out that springerocystid eocrinoids had an asymmetrical arrangement of 'arm' facets and a theca with stem and peristome offset as in paracrinoids. *Cryptocrinites*, another eocrinoid, has a similar asymmetric theca but has no discernible asymmetry of 'arm' facets. Thus, although paracrinoids are unusual in having brachioles arising from just one side of the ambulacrum their relationship as cystoids is to my mind unambiguous. A cladogram of character distribution (text-fig. 9B) can be constructed to suggest how paracrinoids relate to certain other cystoid groups.

#### FOSSIL EVIDENCE IN DETERMINING RELATIONSHIPS AMONGST LIVING GROUPS

The idea that relationship of living groups can be determined by looking at the fossil record is, at first glance, very appealing. After all, the fossil record is often thought to provide the only tangible evidence of evolution. And yet, if this is so, why has the advancement in palaeontological knowledge

TABLE 1. Character distribution for selected genera of paracrinoid and other cystoids as shown in text-fig. 9b

Primitive	Derived
1. Polyplated stalk	Holomeric stem composed of thin discoidal columnals
2. Basals undifferentiated	Three basals
3. Ambulacra forming an integral part of the thecal wall	(a) Ambulacra erect, exothecal, attached to facets close to the peristome (b) Ambulacra secondarily recumbent, overlying thecal plates
4. Periproct in C/D interray	Periproct lateral in B/C interray
5. Oral area flush with theca	Oral area a spout-like projection
6. Oral area composed of seven plates, six of which surround the peristome	(a) Oral area composed of six plates all surrounding the peristome (b) Oral area composed of four plates around the peristome
7. Thecal plates numerous, new plates added by intercalation	(a) Thecal plates relatively few, not intercalated during growth (b) Thecal plates reduced to three cycles
8. Brachioles arise from both sides of the ambulacra	Brachioles arise from only one side of each ambulacrum
9. Peristome at apex of theca, opposite the stem	Peristome offset; periproct at apex of theca, opposite the stem
10. Ambulacra and brachioles biserial	Ambulacra and brachioles uniserial
11. Ambulacra more or less straight	Ambulacra curved in a solar direction
12. Pentamer symmetry of rays	Two primary rays: (a) unbranched; (b) both branched; (c) one only branched
13. Globular or sac-like theca	Biconvex theca
14. Plates without internal pits	Internal (respiratory) pits
15. Plates smooth	Plates strongly ornamented with radially arranged and internally excavated ribs
16. Plates convex	Plates concave
17. Brachioles erect	Brachioles recumbent
18. Peristome exposed	Peristome covered by oral plates

of echinoderms not been reflected in an increased understanding about the interrelationships amongst living groups? Since 1900 many new fossil echinoderm groups have been described, yet taking just the five extant classes (text-fig. 7) we are no nearer understanding how they are interrelated than Bather (1900) was. Indeed, uncertainty has actually increased; whereas Bather accepted eleutherozoan echinoderms as a natural group, the failure of palaeontology to identify obvious intermediates between asterozoan and echinozoan eleutherozoans has resulted in less certainty about the relationship of these two groups (text-fig. 7). One can only conclude that historically, palaeontology has provided no input to the unravelling of relationship amongst living echinoderm classes. This, to some extent, may be because, until recently, there has not been the methodology to use the fossil record constructively, but it is also because the fossil record cannot by itself resolve problems of relationship.

One of the difficulties of working with fossils is that only skeletal morphology is generally preserved. In comparison with the wealth of anatomical, genetic, biochemical, and embryological data available in living echinoderms, fossils can provide only a small part of that information. It is therefore not surprising that there is an increased uncertainty about affiliation amongst fossil groups. For example, in echinoderm classification the position of the radial water vessel, whether external or internal, is a character of some importance. Embryology shows quite unequivocally that the internal position of the radial water vessel is secondary and derived during development from an originally external position (MacBride 1914). Yet, as the radial water vessel is composed entirely of soft tissue, when we look at fossils it is open to argument where the radial water vessel was situated. Bather (1915), Ubahs (1975), and myself (in Paul and Smith 1984) have all argued that in edrioasterids the radial water vessel lay external to the flooring plates. However, Bell (1975, 1977) has argued that edrioasterids had an internal radial water vessel. Although one or other side may present more convincing arguments, there is no way in which we can be absolutely certain unless a specimen with preserved soft tissue is found. Therefore, at least some characters that are crucial in identifying relationship amongst living echinoderms are absent or unprovable in fossil groups. Fossils preserve only a small proportion of all character attributes available in living groups.

A second reason why palaeontology has had little or no impact on resolving relationships stems from the fact that fossils rarely contain a more informative pattern of character distribution than is present in extant groups. The following example will help to explain what is meant. Consider three extant groups A, B, and C each of which is quite distinct in having a number of autapomorphies. In addition, let us assume that only one synapomorphy 'j' can be discovered which identifies B and C as sister groups. Can we get more information from looking at the character distribution in fossils? As we go back in time the three groups will appear to become less distinct from one another as autapomorphic characters 'disappear'. Eventually a point will come when groups B and C no longer exist as distinguishable taxa since their members are plesiomorphic with respect to all characters save for character 'j' which distinguishes them from group A members. So, although fossils may show that extant groups were more similar due to plesiomorphy in the past, the only characters which allow us to identify sister groups (synapomorphies) are very often already known from comparative anatomy of the living members. The fossil record simplifies by removing autapomorphies but cannot generally add to the number of synapomorphies. There are, of course, exceptions where the fossil record can show characters to be more general in distribution than might be suspected from living groups or might identify structures as homologous which are highly modified in living groups, and these are discussed below. In general, however, fossils contain a no more informative pattern of character distribution than is present in extant groups.

Fossils provide information about their geological age from their stratigraphical occurrence, yet as Nelson and Platnick (1981) have argued this has no value on its own in determining relationship. Ideas on relationship are not based initially on stratigraphical occurrence but on comparative skeletal morphology. Where the stratigraphical sequence agrees with deductions based on comparative morphology then the fossil record is accepted as an adequate guide to relationships. Where comparative morphology and the stratigraphic record conflict then the fossil record is dismissed as incomplete. Clearly then, the fossil record on its own is no guide to relationship, since it

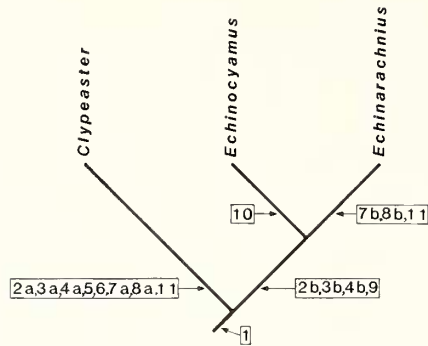
is accepted as adequate when in agreement but rejected as inadequate when in conflict with comparative anatomy. All that can be claimed is that if the fossil record agrees with a hypothesis of relationship based on morphology (and one would hope that it might) then yet another piece of evidence has been added in support. If it conflicts then the hypothesis may still be correct, since the fossil record could be incomplete.

Turning now to a practical example, clypeasteroids are believed to have evolved in the Tertiary and have an excellent fossil record. Here then is a group where one might reasonably expect the fossil record to provide additional evidence on how clypeasteroids are interrelated and from whence they originated. In order to simplify matters I shall just discuss three extant clypeasteroids, *Clypeaster*, *Echinocyamus*, and *Echinarachnius*, as representatives of the groups Clypeasterina, Fibulariina, and Scutellina respectively. Analysis of character distribution amongst these three clypeasteroids gives the cladogram in text-fig. 10. Outgroup comparison suggests that their closest living relatives are the cassiduloids (holectypoids are rejected since the character used by Durham *et al.* (1966) to unite holectypoids and clypeasteroids was the presence of a lantern, which is plesiomorphic). Morphologically, *Echinocyamus* is the least specialized of the three (i.e. it has the fewest autapomorphies) and both *Clypeaster* and *Echinarachnius* pass through a developmental stage in which they resemble fibulariids. It is therefore most parsimonious to assume that at some period in the past cassiduloids and clypeasteroids shared a common ancestor which they did not share with any other living group and that *Echinocyamus*, with its more generalized body plan, has diverged least from the latest common ancestor of living clypeasteroids. All so far has been deduced without reference to the fossil record.

If fossil clypeasteroids are examined then we find species with either clypeasterinid, fibulariinid, or scutelinid autapomorphies, a few with characters common to both fibulariinid and scutelinids but without any autapomorphies of either group, and one genus, *Togocyamus*, which has a few basic clypeasteroid features but no autapomorphies of any one group or pair of groups. *Togocyamus* is, as was predicted from character distribution amongst extant groups, rather like *Echinocyamus* in shape and was originally classified as a fibulariid. However, from the description given by Kier (1982), *Togocyamus* clearly lacks all the advanced characteristics of perignathic girdle and pore arrangement that distinguish fibulariids from other groups. So far then the fossil record has simply confirmed what was already predicted from the living groups. What about the relationship of clypeasteroids to cassiduloids—can the fossil record provide evidence of transitional forms linking these two groups? Here, however, we run into the basic problem of how to recognize a fossil as ancestral to the clypeasteroids when clypeasteroids are recognized by the presence of multiple ambulacral pores on adoral plates. All that we can be certain of is that the ancestor will have had the characteristics that are common to both cassiduloids and clypeasteroids, but none of the characteristics unique to clypeasteroids. Identifying *Togocyamus* as a primitive clypeasteroid has not made the relationship of clypeasteroids and cassiduloids any more obvious.

The conclusions that are to be drawn from this example are threefold. First, palaeontology has corroborated the hypothesis of relationship based on living groups. Secondly, it has confirmed the statement on generality of characters since *Togocyamus* conforms to the concept of a primitive clypeasteroid based on character distribution amongst living groups. Thirdly, the recognition of fossils as primitive members of an extant group does not in this case lead to any clearer understanding about their relationship to other groups. The fossil record has only been able to corroborate what was already known about character distribution and has, as yet, provided no tangible link with cassiduloids. The evidence for clypeasteroid–cassiduloid relationship comes from character analysis of the living groups.

So far I have tried to show that fossil echinoderms have done little more than corroborate hypotheses of relationship that can be deduced from the study of living groups. However, the fossil record does contain information on character distribution that is not available to neontologists and has a very positive role to play in the formulation of hypotheses of relationship as has clearly been shown by Patterson (1981). It is these positive aspects that are worth stressing since only through them will palaeontology be able to make a substantial contribution to our understanding of relationship.



TEXT-FIG. 10. A cladogram for three extant clypeasteroid genera. Characters 1–11 are given in Table 2. For discussion see text.

TABLE 2. Character distribution for three genera of clypeasteroid echinoid

Primitive	Derived	Occurrence
1. One tube foot per ambulacral plate	Multiple tube feet on ambulacral plates	<i>Clypeaster</i> , <i>Echinocyamus</i> , <i>Echinarachnius</i>
2. Lantern muscles attached to amb. and Iamb. plates	(a) Lantern muscles attached to Iamb. plates only (b) Lantern muscles attached to amb. plates only	<i>Clypeaster</i> <i>Echinocyamus</i> , <i>Echinarachnius</i>
3. Lantern absent in adults	(a) Clypeasterid-type lantern (b) Fibulariid-type lantern	<i>Clypeaster</i> <i>Echinocyamus</i> , <i>Echinarachnius</i>
4. No internal buttressing	(a) Buttressing of concentric laminae plus pillars (b) Buttressing of radial partition with or without pillars	<i>Clypeaster</i> <i>Echinocyamus</i> , <i>Echinarachnius</i>
5. Ambulacral plating simple	Petals with pseudo-compounding	<i>Clypeaster</i>
6. Four gonopores	Five gonopores	<i>Clypeaster</i>
7. No food groove system	(a) Simple food grooves lacking tube feet (b) Branched food grooves lined with tube feet	<i>Clypeaster</i> <i>Echinarachnius</i>
8. Tooth with fibulariid LNPS system	(a) Tooth with clypeasterid LNPS system (b) Tooth with echinarachniid LNPS system	<i>Clypeaster</i> <i>Echinarachnius</i>
9. No buccal tube feet	Buccal tube feet	<i>Echinocyamus</i> , <i>Echinarachnius</i>
10. Accessory tube feet distributed over oral plates	Accessory tube feet arranged in discrete bands	<i>Echinocyamus</i>
11. Test egg-shaped	Test discoidal to hemispherical	<i>Clypeaster</i> , <i>Echinarachnius</i>



1. Fossils can sometimes show that a character absent in a living group was present in fossil species of that group, i.e. they can show a character to be more general in distribution than is apparent from the study of living forms. For example, although echinoids, holothuroids, and asteroids all possess a madreporite, most living ophiuroids do not and show no evidence of ever having had one even during embryological development (see Hendler, 1979). Lower Palaeozoic ophiuroids do, however, possess a madreporite thus showing that the presence of a madreporite is a characteristic originally shared by all elutherozoans and that it has been secondarily lost in the great majority of crown group ophiuroids.

The fossil record is particularly helpful where synapomorphic characters have been lost completely in one branch of a monophyletic group. This can occur through developmental foreshortening. Often, fossil members of the group (those with at least one autapomorphy of the crown group) may retain synapomorphic characteristics that the group shares with its extant sister group but which have been lost in all living members. As an example of this consider the living crinoid group Holopodina. Holopodinids are a small group of minute and highly modified crinoids that live cemented to hard substrata in deep oceanic waters. They have no remnant of a stem, nor identifiable cup plating and because of their habitat nothing is known about their development. They are so modified that it is impossible to be certain about which group of articulate crinoids represents their sister group. When fossil articulate crinoids are considered we find groups that are less modified. The eudesicrinids have many of the autapomorphic characters of living holopodinids but lack fused plating. Another fossil group, the cyrtocrinoids, possess a few characteristics that are autapomorphies of living holopodinids but have not lost their stem. Because both eudesicrinids and cyrtocrinoids possess some characteristics that are unique to living holopodinids they must belong to the holopodinid stem group. The cup plating and stem morphology in fossil stem group members provide characters which have been lost from living members and which allow us to identify hyocrinids as the most likely sister group of the holopodinids.

2. The fossil record can sometimes provide the sense of direction to a morphological series which is otherwise ambiguous. For example, living echinoids have either solid or hollow spines. Solid spines are found in all cidaroids and in some euechinoids whereas hollow spines occur only in euechinoids. From generality of distribution, and as on other evidence cidaroids are the primitive sister group of euechinoids, it would be reasonable to assume that solid spines were primitive and that the evolution of hollow spines within the euechinoids might be a synapomorphy. In fact the fossil record shows that stem group echinoids, stem group cidaroids, and many early euechinoids had hollow spines. Solid spines have therefore twice evolved independently.

3. Fossils can help in the identification of homologous structures in groups that have become highly modified. Sister groups may become so different by the evolution of autapomorphies and the extinction of intermediates that it can sometimes be difficult to identify homologous structures correctly within these groups. Living crinoids are very different from their nearest living relatives, the asteroids, because a great many intermediate forms have become extinct. In the search for homologous structures the fossil record can often be useful since it is sometimes possible to trace a highly modified structure back to something more simple. By doing this we can show that the adambulacral plates in extant asteroids are probably homologous with cover-plates in crinoids, brachioles in cystoids, lateral arm plates in ophiuroids, and primary ambulacral spines in echinoids. Here the fossil record is a slightly better guide to homology than study of either development or comparative anatomy.

4. The earliest stratigraphical age at which a group is known to exist gives the latest date at which the group became split from its primitive sister group, but does not date the timing of the split more precisely since no lower limit can be fixed. However, the better the fossil record, the closer this date corresponds to the definitive time of splitting. The relative timing of the appearance of different groups should correspond to the sequence in which they appear in a cladogram of character distribution. If it does, or more or less does, then there is no problem. If it is largely incongruent then either the fossil record is poor or the cladogram is false, or both.

5. Fossils allow the sequencing of crown group autapomorphies. Every crown group is identified

by the occurrence of one or more synapomorphies which all its members share. These characters are the autapomorphies of that group. Analysis of character distribution amongst extant members of the crown group will identify a nested hierarchy which represents the pattern of character acquisition within the crown group. It will not, however, provide any method for the sequencing of crown group autapomorphies. Only by analysing character distribution within members of the wholly extinct stem group can the pattern of autapomorphy acquisition be identified. For example, living cidaroids have some characters which are common to all echinoids or to echinoderms in general (a water vascular system, a lantern, a test composed of ten ambulacral and ten interambulacral columns, articulating spines, pedicellariae, etc.) together with some unique characters. Of these unique characters, some are common to all living cidaroids (e.g. U-shaped teeth, an upright lantern with a small foramen magnum, solid spines, a perignathic girdle of apophyses) whilst others are found only in certain subgroups (e.g. perforate tubercles, conjugate pores). By analysing character distribution amongst living groups it is possible to derive a hierarchical pattern for those characters of restricted occurrence from which the sequence of character acquisition can be interpreted. But characters unique to the whole group cannot be sequenced since all living members share them. It is only by looking at the pattern of character distribution amongst members of the extinct stem group that we can identify the sequential acquisition of characters autapomorphic to the crown group. In this way it is possible to determine that in cidaroids a perignathic girdle of apophyses was acquired before an upright lantern with a shallow foramen magnum and that solid spines, a rigidly sutured test, and U-shaped teeth were all later acquisitions.

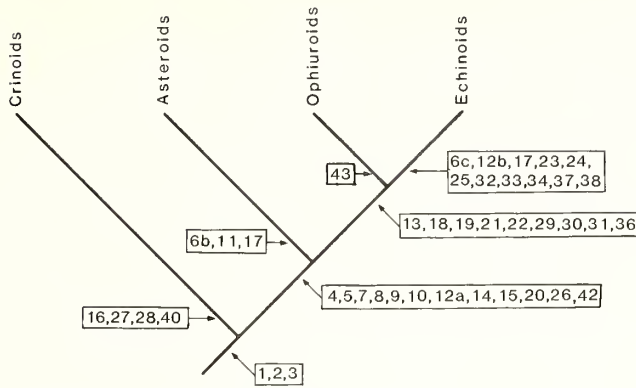
#### A PHYLOGENETIC APPROACH TO THE CLASSIFICATION OF ECHINODERMS

In the preceding sections I have briefly outlined the way in which fossil echinoderms have been treated in the past and have attempted to identify precisely what the fossil record can and cannot tell us about relationships. In the past, fossil echinoderms have tended to be classified in a subjective and uninformative manner. As more and more fossil groups have been raised to high taxonomic levels the hierarchical nature of classification schemes has been disrupted and its information content diminished, while no progress has been made in unravelling relationships of living echinoderms. Furthermore, reasons have been given why fossils alone cannot provide direct evidence concerning the relationship of extant groups, although they can often help in the process of discovering these relationships. It therefore seems that a fairly drastic reappraisal of how fossil echinoderms should be classified is necessary. This last section outlines how fossils can be incorporated more informatively into a classification. Again none of the ideas presented here is new. The basic methodology by which fossils could be classified was discussed by Hennig (1966) and there have been several notable contributions to this subject since then (e.g. Nelson 1972, 1974; Patterson and Rosen 1977; Wiley 1979).

Since a knowledge of fossil echinoderms has made little positive contribution to our understanding of how the principal extant groups are interrelated and indeed has often been interpreted in a misleading way, it seems sensible to construct a hypothesis of relationship on the basis of character distribution derived from comparative anatomy and developmental biology of extant species. Fossils then provide a record of character distribution in the past which can be used to check statements of homology, identify synapomorphic characters that have been lost through developmental fore-shortening, and identify the sequence of character acquisition where more than one autapomorphy identifies an extant group. The cladogram derived for living groups can then be used as a primary framework to which fossil groups can be added in their correct position.

##### *The primary framework*

Table 3 lists a variety of important characters shared amongst the five extant classes of echinoderm. These are drawn from published descriptions of embryological development and from gross comparative anatomy. The pattern of character distribution is quite unambiguous for four of the five

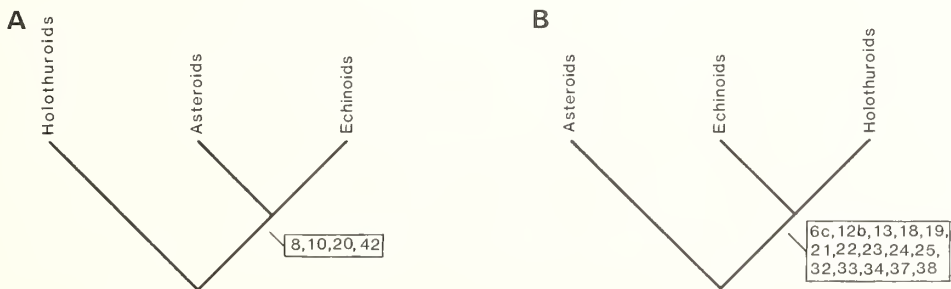


TEXT-FIG. 11. Cladogram for four of the five extant classes of echinoderm based on embryology and comparative anatomy. Characters 1-43 are given in Table 3.

classes (text-fig. 11). It identifies crinoids as a primitive sister group to the other three and asteroids as the primitive sister group to ophiuroids plus echinoids. This is in full agreement with the conclusions of MacBride (1914) and Hyman (1955).

The phylogenetic position of holothuroids is less obvious and needs careful analysis. Holothuroids share a number of derived characters with ophiuroids and echinoids and several more with only echinoids. However, there are a number of other derived characters that are common to asteroids, ophiuroids, and echinoids or only to ophiuroids and echinoids which are not found in holothuroids. To try to resolve the phylogenetic position of holothuroids the problem can be reduced to a number of three taxon problems and the alternatives compared.

First, let us ignore ophiuroids and consider whether holothuroids or asteroids are phylogenetically the more closely related to echinoids. The alternative cladograms are given in text-fig. 12. It is quite evident that there are many more derived characters that suggest that holothuroids and echinoids are sister groups than suggest that asteroids and echinoids are sister groups. It is therefore worth examining the four characters that suggest asteroids and echinoids to be more closely related and which on the grounds of parsimony alone would be rejected. The presence of a genital rachis and multiple gonads, as found in asteroids and echinoids, is undoubtedly a derived character while the single gonad and gonopore of holothuroids is primitive. However, primitive stem group echinoids have but a single gonopore and, by inference, a single gonad (Smith 1984); therefore the genital rachis

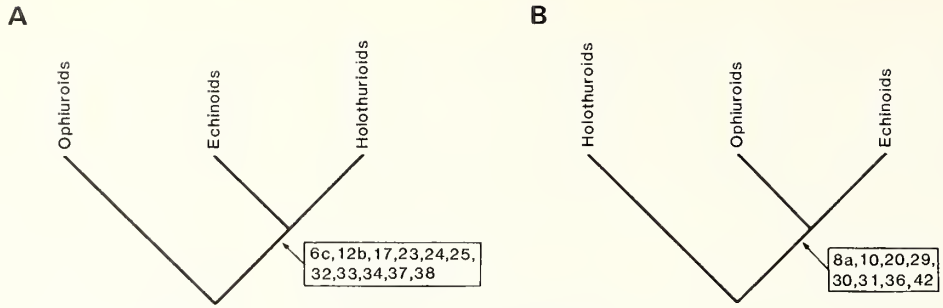


TEXT-FIG. 12. A three taxon cladogram to resolve the relationship of holothuroids to asteroids and echinoids. Characters 1-43 are listed in Table 3.

TABLE 3. Primitive and derived character states in extant echinoderm classes. The classes that possess derived character states are given in the third column

Primitive	Derived	Occurrence
1. Skeleton absent	Calcite skeleton of stereom	Crinoids, Asteroids, Ophiuroids, Echinoids, Holothuroids
2. Larval development bilaterally symmetrical	Development of right-hand side larval coeloms suppressed	Crinoids, Asteroids, Ophiuroids, Echinoids, Holothuroids
3. Without radial symmetry	With radial (pentamer) symmetry	Crinoids, Asteroids, Ophiuroids, Echinoids, Holothuroids
4. Larva without processes	Larva with incipient processes (auricularia)	Asteroids, Ophiuroids, Echinoids, Holothuroids
5. Hydropore opening simple	Hydropore opening a calcified body (madreporite)	Asteroids, Ophiuroids, Echinoids, Holothuroids
6. Definitive anus opens lateroventrally	(a) No anus in adults (b) Definitive anus opens laterodorsally in B/C inter-radius (c) Definitive anus opens dorsally at site of larval anus	Ophiuroids, some Asteroids Some Asteroids Echinoids, Holothuroids
7. Adult attached	Adult free-living	Asteroids, Ophiuroids, Echinoids, Holothuroids
8. Ambulacral plates added at tip of radial water vessel	(a) Radial water vessel tip associated with terminal plate; new ambulacral plates added adorally to terminal plate (b) Ambulacral plates wanting	Asteroids, Ophiuroids, Echinoids Holothuroids
9. Tube feet arise directly from the radial water vessel	Tube feet arise from lateral branches of the radial water vessel	Asteroids, Ophiuroids, Echinoids, Holothuroids
10. No articulating spines	Articulating spines	Asteroids, Ophiuroids, Echinoids
11. Larval vestibule formed	No larval vestibule formed	Asteroids
12. Aboral surface greatly enlarged	(a) Aboral and oral surfaces equally developed (b) Aboral surface greatly reduced	Asteroids, Ophiuroids Echinoids, Holothuroids
13. Entoneural nerve plexus present	Entoneural nerve plexus absent	Ophiuroids, Echinoids, Holothuroids
14. Entoneural nerve plexus as primary motor coordination system	Ectoneural nerve plexus as primary motor coordination system	Asteroids, Ophiuroids, Echinoids, Holothuroids
15. No hyponeural sinuses	Hyponeural sinuses present	Asteroids, Ophiuroids, Echinoids, Holothuroids
16. Right hydrocoel present but vestigial in development	Right hydrocoel does not form during development	Crinoids, Holothuroids
17. Tube feet without internal ampulla	Tube feet with internal ampulla	Asteroids, Echinoids, Holothuroids
18. Larva attaches by pre-oral lobe	Larva unattached	Ophiuroids, Echinoids, Holothuroids

Primitive	Derived	Occurrence
19. Radial water vessel and nerve external	Radial water vessel and nerve enclosed by epineural folds	Ophiuroids, Echinoids, Holothuroids
20. Single internal gonad arising from genital stolon	Multiple internal gonads arising from genital rachis surrounding axial complex	Asteroids, Ophiuroids, Echinoids
21. No epineural sinuses	Epineural sinuses present	Ophiuroids, Echinoids, Holothuroids
22. Entomesoderm forms in gastrula from archenteron	Entomesoderm starts to form in blastula from one side of the wall before embolic invagination	Ophiuroids, Echinoids, Holothuroids
23. Radial water vessel grows radially	Radial water vessel grows meridionally	Echinoids, Holothuroids
24. Tube foot wall uncalcified	Tube foot wall with spicules	Echinoids, Holothuroids
25. Suckered tube feet without skeletal disc plates	Suckered tube feet with skeletal disc plates	Echinoids, Holothuroids
26. Larva lacks a mouth	Larval mouth forms	Asteroids, Ophiuroids, Echinoids, Holothuroids
27. Gonads internal	Gonads external, on arms	Crinoids
28. Ambulacra forming integral part of the theca	Ambulacra extending free of theca as arms	Crinoids
29. Larva with short processes	Larva with elongate processes	Ophiuroids, Echinoids
30. Larval processes not supported by calcite rods	Larval processes supported by calcite rods	Ophiuroids, Echinoids
31. Larval mouth retained as adult mouth but migrates to the left during development	Larval mouth lost during development; adult mouth opens to the left of the larval mouth	Ophiuroids, Echinoids
32. No peripharyngeal coelom	Peripharyngeal coelom	Echinoids, Holothuroids
33. No perianal coelom	Perianal coelom	Echinoids, Holothuroids
34. Haemal system rudimentary, an open lacuna network	Haemal system extensive and well developed, with a rete mirabile	Echinoids, Holothuroids
35. Axial complex fully developed	Axial complex absent or vestigial	Holothuroids
36. Adoralmost ambulacral ossicles forming a semi-flexible oral frame	Adoralmost ambulacral ossicles modified into a muscular jaw apparatus	Ophiuroids, Echinoids
37. Adoralmost ossicles remain an integral part of ambulacral plating	Adoralmost ossicles internal and surround oesophagus	Echinoids, Holothuroids
38. Radial ambulacral muscles interossicular and segmented	Radial ambulacral muscles internal and unsegmented	Echinoids, Holothuroids
39. Ambulacral ossicles present	Ambulacral ossicles lost	Holothuroids
40. Blastopore remains as larval anus	Blastopore closes after formation of archenteron	Crinoids
41. No polian vesicles	Polian vesicles	Asteroids, Ophiuroids, Holothuroids
42. No Tiedemann's bodies	Tiedemann's bodies	Asteroids, Ophiuroids, Echinoids
43. Vestibule sealed off from exterior during development	Vestibule remains open	Ophiuroids



TEXT-FIG. 13. A three taxon cladogram to resolve the relationship of holothuroids to echinoids and ophiuroids. Characters 1–43 are listed in Table 3.

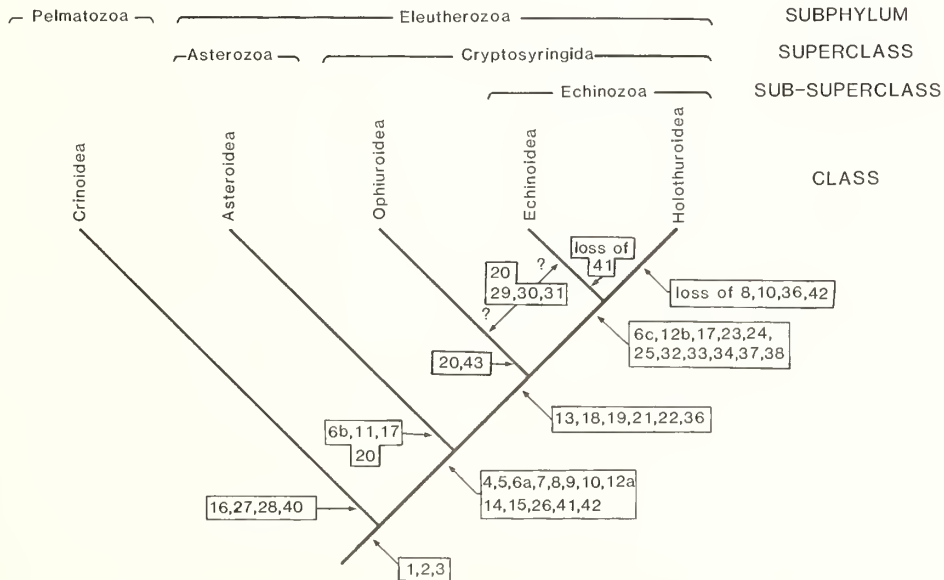
and multiple gonads must have evolved independently in echinoids and asteroids. This character can therefore be rejected as being a convergence on the basis of fossil evidence. Tiedemann's bodies are present in ophiuroids as well as in asteroids and echinoids. Their absence in holothuroids may be a secondary loss, since these bodies perform the same function as the axial complex (Bachmann and Goldschmidt 1980) which is vestigial or absent in holothuroids. The two remaining characters common to asteroids and echinoids but not to holothuroids are the presence of terminal plates (oculars), which appear early in development, and the presence of articulating spines. Neither character carries much weight as the skeleton of holothuroids has become highly modified and is usually reduced to rudimentary spicules. The development of the few living holothuroids that retain a skeleton of thin imbricate plates has never been reported and it is therefore impossible to recognize these characters in holothuroids. In view of the outstanding evidence in favour of placing asteroids as the primitive sister group of holothuroids plus echinoids, it seems reasonable to assume that living holothuroids have lost both spines and apical plates as a consequence of the profound simplification of their body wall skeleton.

The only question remaining then is, comparing ophiuroids, echinoids, and holothuroids, which pair is the more closely related? Derived characters exist that link holothuroids and echinoids and which link echinoids and ophiuroids but none exist linking ophiuroids and holothuroids. Therefore we need consider only two of the three possible cladograms (text-fig. 13). Both seem to be supported by a number of characters. However, of those identifying ophiuroids and echinoids as a group, four (the presence of a genital rachis and multiple gonads, Tiedemann's bodies, terminal (ocular) plates, and articulating spines) have already been rejected on the strength of the preceding cladogram, and cannot be used. Of the remaining four characters, one, the presence of homologous ambulacral ossicles modified into a jaw apparatus, is questionable because holothuroids have such a modified and reduced larval skeleton that such a structure might easily have been lost. The internal calcareous ring may be homologous with some plates of the jaw apparatus but there is too little evidence to be certain. This character can be rejected on fossil evidence, however, since the stem group holothuroid *Rotasaccus* has a fully developed lantern which is in all details, save for tooth structure, identical with that of echinoids (Haude and Langenstrassen 1976). Three characters remain that are incongruent: the absence of a pluteus larva with elongate processes, the absence of skeletal rods supporting the larval processes, and the retention of the larval mouth throughout development. The first two characters are interconnected since the larval skeleton forms to support processes that develop in the pluteus larva to extend the ciliated bands. Neither the processes nor the skeleton are identical in echinoids and ophiuroids. The ophiopluteus has no pre-oral processes and the main locomotory processes that develop early on are the posterolateral ones, whereas in the echinopluteus, elongate pre-oral processes are present, and the main locomotory processes are the post-oral ones. The posterolateral processes either appear much later in development and remain small or are absent

altogether. The ophiopluteus has just two centres of calcification from which calcite rods grow, one on either side, whereas the echinopluteus has five, two on the left, two on the right, and an anterior V-shaped rod for the pre-oral processes. There is therefore a distinct possibility that elongation of the small processes common to all eleutherozoan larvae occurred independently in ophiuroids and echinoids.

The evidence concerning the phylogenetic position of holothuroids, although ambiguous, definitely tends to favour echinoids and holothuroids as being sister groups. If I have identified the ophiocistioid *Rotasaccus* correctly as a stem group holothuroid then the presence of a lantern so similar to that of echinoids in *Rotasaccus* convinces me that echinoids and holothuroids are sister groups and that holothuroids have undergone fairly major change through reduction of the body skeleton since the two groups became separated. However, it must be said that the available biochemical evidence concerning sterols (Bolker 1967; Goad *et al.* 1972), phosphorus carriers (Florkin 1952), and collagen (Matsumura *et al.* 1979) do not support this and indicate that echinoids and ophiuroids share a greater similarity. As I lack expertise in this field I cannot assess these data from a cladistic standpoint and therefore cannot tell what sort of similarity it is that echinoids and ophiuroids share.

The result of analysing character distribution amongst living groups of echinoderms gives the nested hierarchy shown in text-fig. 14. If, following historical precedence, the five extant groups are given class status then the hierarchical pattern must dictate the higher classification of the Echinodermata. Names are available for all but one group. The Echinodermata can be divided into two subphyla, Pelmatozoa for the crinoids and Eleutherozoa for the asteroids, ophiuroids, echinoids, and holothuroids. (Haugh and Bell (1980) rejected the Eleutherozoa as a monophyletic taxon on the grounds that the 'absence of stem' was a non-character, an argument which comparative embryology refutes.) At superclass level we can use the name Asterozoa for the asteroids but no name has ever been proposed for the group comprising the Ophiuroidea, Echinoidea, and Holothuroidea. I therefore propose to name this group Cryptosyringida (derivation—Greek *Kryptos*, hidden;



TEXT-FIG. 14. The most parsimonious cladogram for the five extant classes of echinoderm with a suggested hierarchical classification. Characters 1–43 are given in Table 3.

*Syringos*, a pipe or fistula, in allusion to the fact that the radial water vessel and radial nerve becomes covered during development). Finally, the echinoids and holothuroids are grouped together in the Echinozoa at sub-superclass level.

*Incorporating fossil groups into the primary classification*

The concept of crown and stem groups becomes indispensable when dealing with the classification of fossil groups. Monophyletic groups of living echinoderms belong to a whole series of increasingly more generalized crown groups of which the most narrowly defined contains only members of that group and no others. Fossil echinoderms also belong to a whole series of increasingly more generalized crown groups but, with one exception, all fossils also belong to a single stem group. In systematics the pattern of character distribution is used to determine at what level a species or group of species belong. Neontologists search for the most narrowly defined crown group whereas palaeontologists attempt to discover the unique stem group that each fossil belongs to. The level of generality for stem groups is as variable as it is for crown groups. For example, the Cretaceous cidarid *Stereocidaris sceptifera* belongs to the stem group of the genus *Stereocidaris* whereas the lower Cambrian helicoplacoid *Helicoplacus gilberti* is so generalized that it is a member of the stem group of the Echinodermata.

Each stem group may contain one or many members. In some cases the stem group might be quite small, as in echinoids where there are approximately 125 known stem group species but almost 7,000 crown group species. In other cases—for example, Pelmatozoa—the stem group is enormous compared with the crown group and includes all cystoids and all crinoids except the Articulata. The members of each stem group possess at least one but not all of the autapomorphies that define the crown group. It is therefore possible to arrange fossils in the stem group according to the distribution of crown group autapomorphies (see Patterson and Rosen 1977; Wiley 1979). The most primitive will have just one autapomorphy, the most advanced will have all but one. However, a few fossils will belong not to the stem group but to the crown group. These will have all the autapomorphies that define the crown group but none of the autapomorphies of any subdivision of the crown group and will include the first member of the crown group.

Because groups can be distinguished as discrete entities only when they have evolved a new character, the maximum resolution that we can hope for is to distinguish one or a group of fossils at the appearance of each new crown group autapomorphy. Those fossils which all have the same crown group autapomorphies represent a monophyletic side branch from the stem line. The number of autapomorphies that can be identified limits the number of stem groups that can be identified, yet although this is presumably finite, there is no way of predicting how many can be recognized. Each side branch of the stem group (zwischenkategorien of Hennig 1969; plesion of Patterson and Rosen 1977) may contain only a single species or may contain a large number of species, in which case character distribution can be analysed to discover pattern and phylogenetic relationship within the side branch. Each side branch, being a monophyletic group, can be named and classified from the species level up. Their nominal categorial rank is unimportant and is best based on diversity or historical precedence. The groups which make up the stem group can then be listed in an order corresponding to the acquisition of crown group autapomorphies and incorporated into the primary classification as recommended by Wiley (1979).

As palaeontologists are concerned with pattern recognition in stem groups, it is possible that having a name for each stem group might be quite useful for communicating precisely about which group of fossils are under investigation. To avoid further proliferation of names, it is probably best if they were referred to as stem group cidaroids, stem group isocrinids, etc., but if a widely used name is available I can see no objection to its being used. For example, when I analysed the stem group echinoids (Smith 1984) the traditional group Perischoechinoidea seemed to correspond more or less to the stem group and I suggested retaining Perischoechinoidea for the paraphyletic stem group of the Echinoidea.

Some traditional fossil groups are truly monophyletic and can be incorporated into the stem group in their correct position. Others, however, turn out to be paraphyletic since they were defined on the



absence of one or more crown group autapomorphies. These will eventually have to be abandoned in favour of groups which are more informative about character distribution.

The status within this classification of the principal fossil groups of echinoderm recognized in the *Treatise* (Moore and Teichert 1978) will now be outlined:

(i) *Carpoids* ('Classes' Ctenocystoidea and Stylophora and 'Orders' Soluta and Cincta). Carpoids are all basically asymmetric, without a trace of radial symmetry and either lack ambulacra or have a single exothecal appendage. They all have a single feature, their calcite endoskeleton, which they share with crown group echinoderms. However, Jefferies (1981) believes that Stylophora show evidence of gill slits and a post-anal tail and should therefore be classified as stem chordates. If this proves to be correct then the other carpoids may be stem chordates, stem echinoderms, or stem (chordates plus echinoderms). Further work is required to resolve the phylogenetic position of these groups and I shall not consider them further.

(ii) *Helicoplacoids* ('Class' Helicoplacoidea). There are only two or possibly three genera of helicoplacoids and a handful of species. Their morphology and phylogenetic position has been discussed by Paul and Smith (1984). Helicoplacoids have a laterally positioned mouth, no oral/aboral differentiation of the skeleton and triradial ambulacra. They are stem group echinoderms and have been incorporated into the classification as a plesion with the nominal rank of family (Table 4).

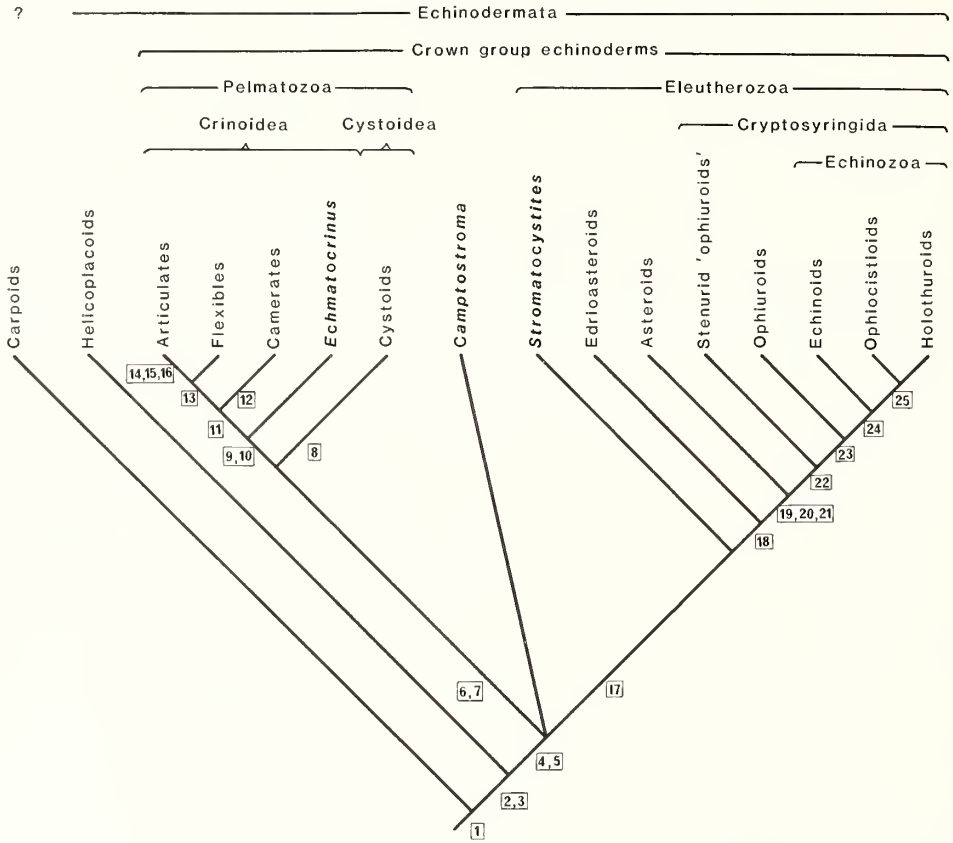
(iii) *Camptostroma* ('Class' Camptostromatoidea). The phylogenetic status of *Camptostroma* has also been discussed by Paul and Smith (1984). *Camptostroma*, represented by a single known species holds a rather important position in the cladogram (text-fig. 15) since it possesses all of the autapomorphies of crown group echinoderms but none of the autapomorphies of either Pelmatozoa or Eleutherozoa. It therefore belongs to the group in which the latest ancestor of crown group echinoderms would be placed.

(iv) Cystoids ('Superclass' Cystoidea = 'Subphylum' Blastozoa). In recent years the cystoids have been split up into a number of high categorical taxa. Some of these are undoubtedly monophyletic (blastoids, paracrinoids) whereas others are apparently paraphyletic (rhombiferans, eocrinoids—see Paul and Smith 1984) and need to be reclassified in a more informative way. Previously the presence or absence of a single character (usually a respiratory structure) has been used to identify groups. Cystoids *sensu lato* are clearly a monophyletic group and their subvective system includes brachioles which are homologues of cover-plate series. The only crown pelmatozoan autapomorphies that they share with extant crinoids are the presence of an elongate dorsal stalk and, in some, the extension of ambulacra free from the thecal wall. They are the most primitive stem group pelmatozoans known. A phylogenetic classification of cystoids should be relatively straightforward and will require a careful analysis of character distribution. Cladistic analysis of this group has never been attempted and holds considerable promise for future research. Cystoids have been incorporated into the classification as a plesion with a nominal rank of Superclass.

(v) *Echmatocrinus* ('Subclass' Echmatocrinea). The single species *E. brachiatus*, represented by some six specimens, is generally taken to be the most primitive member of the Class Crinoidea. It is more advanced than cystoids in that some at least of its ambulacra branch to produce multiple free arms, but it is primitive in comparison with other crinoids in lacking organized thecal plating or stem plating. The Class Crinoidea is monophyletic and corresponds to the crown group plus part of the stem group of the Pelmatozoa. *Echmatocrinus* is the most primitive-known crinoid and is incorporated into the classification as a plesion with generic rank.

(vi) Palaeozoic crinoids ('Subclasses' Inadunata, Camerata, and Flexibilia). The structure of this part of the stem group is the least satisfactory. This is because, although the Camerata and Flexibilia are probably monophyletic groups, the Inadunata is unquestionably a paraphyletic grouping of 'primitive' crinoids that contains the ancestors of camerates, flexibles and articulates (crown group Pelmatozoa). A paraphyletic group such as the Inadunata can only be arbitrarily defined and is undesirable since paraphyletic groupings simply mask the pattern of character acquisition within the stem group. At present only the relative positions of the Camerata and Flexibilia can be shown in a cladogram (text-fig. 15). The inadunates include stem (Camerata + Flexibilia + Articulata), stem

(Flexibilia + Articulata), and stem (Articulata). They represent one of the outstanding areas of ignorance in echinoderm phylogeny and future palaeontological research should be directed towards discovering the pattern of character distribution within inadunates and partitioning this grouping into monophyletic groups. With increasing understanding of the inadunates more plesion categories will be added to the classification in Table 4 between *Echmatocrinus* and the Articulata.



TEXT-FIG. 15. Cladogram incorporating some of the more important fossil groups to show how they fit into the classification scheme. All fossil groups can be assigned to a stem group of one of the crown groups identified in text-fig. 14. Characters 1–25 as follows: 1, calcite endoskeleton of stereom; 2, biserial ambulacra forming integral part of body wall; 3, ambulacra arranged radially, around the mouth (triradial); 4, skeleton differentiated into dorsal and ventral surfaces; 5, pentaradial symmetry; 6, free appendages developed carrying extensions of the radial water vessels; 7, dorsal surface modified to form a stalk; 8, brachioles arise from ambulacra; 9, ambulacra extend free of the theca and carry extensions of major body coeloms; 10, ambulacra uniserial and branched; 11, cup plating clearly differentiated from stem plating; 12, arm plates incorporated into tegmen; stout, rigid tegmen; pinnate arms; 13, tegmen flexible with differentiated ambulacral and interambulacral zones; 14, some arm articulations muscular; arms pinnate; 15, mouth opens through tegmen; 16, anal plates lost from cup; 17, dorsal surface generally flat; adults primitively free-living; 18, epispires lost from ventral surface; 19, mouth frame flexible, composed of ambulacral ossicles only; 20, calcified madreporite; 21, cover-plates modified to adambulacral/lateral arm ossicles; 22, adoralmost ambulacral ossicles modified to form jaw apparatus; 23, radial water vessel enclosed; 24, meridional growth pattern; 25, wheel spicules in body wall.

TABLE 4. A phylogenetic classification of the Echinodermata (conventions as in Wiley 1979)

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Phylum Echinodermata
plesion (Family) <i>Helicoplacidae</i>
Subphylum Pelmatozoa
plesion (Superclass) <i>Cystoidea</i>
Class Crinoidea*
plesion (Genus) <i>Echmatocrinus</i>
plesion (Subclass) <i>Camerata</i>
plesion (Subclass) <i>Flexibilia</i>
Subclass <i>Articulata</i>
Subphylum Eleutherozoa
plesion (Genus) <i>Stromatocystites</i>
plesion (Class) <i>Edrioasteroidea</i>
Superclass <i>Asterozoa</i>
Class <i>Asteroidea</i>
Superclass <i>Cryptosyringida</i>
Subsuperclass <i>Ophiuroidea</i>
Subsuperclass <i>Echinozoa</i>
Class <i>Echinoidea</i>
Class <i>Holothuroidea</i>

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\* Phylogenetic analysis of the Inadunata will add a number of plesions between *Echmatocrinus* and *Articulata* in the future.

(vii) Edrioasteroids ('Class' *Edrioasteroidea*). Edrioasteroids are best considered as stem group Eleutherozoa. The most primitive members were unattached (e.g. *Stromatocystites*) and probably common ancestors to all Eleutherozoa. Most edrioasteroids, however, have a number of autapomorphies and represent a monophyletic side branch of the stem group. Most returned to a fixed mode of life attached via their aboral surface. Unlike pelmatozoans, those that elevated themselves above the sea floor did not develop an aboral stem but expanded their oral surface to become pedunculate. Edrioasteroids have been added to the classification as a plesion with nominal class status.

(viii) Cyclocystoids ('Class' *Cyclocystoidea*). These form a small but diverse group characterized by a number of well-defined autapomorphies. They also share a number of autapomorphies with isorophid edrioasteroids, notably uniserial ambulacral flooring plates and a marginal ring with a single layer of peripheral platelets. I therefore now prefer to place them within the edrioasteroids as the sister group of the Isorophida and with a nominal rank of Order.

(ix) Ophiocistioids ('Class' *Ophiocystioidea*). Ophiocistioids share a number of synapomorphies with the Echinozoa. The discovery of the Devonian ophiocistioid *Rotasaccus* by Haude and Langenstrassen (1976) was a most important find, since *Rotasaccus* has the body wall skeleton of a holothuroid but possesses an echinoid-type lantern. This provides evidence that stem group holothuroids possessed a lantern even though it has been lost in all living holothuroids. Ophiocistioids are undoubtedly a paraphyletic group and an analysis of character distribution within this group will lead to a better understanding of the early history of the Echinozoa.

A simplified cladogram that incorporates the more important fossil groups is shown in text-fig. 15 and a scheme of classification derived from this cladogram is given in Table 4. I have followed the recommendation of Patterson and Rosen (1977) in giving plesion categories only nominal rank and the order in which plesions are listed is dictated by the pattern in the cladogram, as formally recommended by Wiley (1979).

Finally, I should like to point out some of the major gaps in our knowledge about the phylogeny of echinoderms. There remains a basic ignorance about the phylogenetic relationships of cystoid groups which a cladistic approach could help to dispel. More seriously, the classification of Palaeozoic crinoids is most unsatisfactory and a careful and searching look at the Inadunata is needed so that this grouping can be abandoned in favour of monophyletic (and therefore more informative) groups. Thirdly, the phylogeny of primitive 'starfish' has yet to be unravelled satisfactorily and promises to be a most rewarding task. The development of cladistic methodology, which is now such a powerful tool in determining relationships, has opened up new and exciting possibilities for making a real advance in our understanding of echinoderm phylogeny.

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